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Parker, S.

98-5-512

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in Chaparral
A literature Review

May
98-5-512

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NEOTROPICAL MIGRATORY BIRDS IN CHAPARRAL

A Literature Review

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Neotropical Migratory Bird in Chaparral

INTRODUCTION

Neotropical migratory birds (NTMB) can be operationally defined as species which breed (at least partially) in North America temperate zones and migrate (at least partially) south of the continental U.S. during non-breeding seasons. California, with its tremendous north-south extent, provides breeding, migratory, and in some cases, wintering habitat for over one hundred species of NTMB species. Located midway along the Pacific coastal corridor, California habitats lie at the northern most edge of certain species range. Some populations of NTMB species which are migratory elsewhere remain in the State yearlong, in some cases exhibiting elevational rather than latitudinal migratory patterns (Sharpley-Evans 1991).

Recent analysis of regional bird censuses (Robbins et al. 1989) and migration count data (Gauthreaux, in press, Hussell et al., in press) from 1961 to 1988, show that population reduction of neotropical migrants are widespread throughout North America.

Two primary factors explain the population decline: forest fragmentation on the breeding grounds and deforestation of wintering habitats (Morse 1980, Terborgh 1989). Many neotropical birds that nest away from the forest edge (forest-interior species) disappear from forests when habitats are subdivided into smaller patches (Finch 1991a). Nests situated along forest edges and in small forest patches experience greater rates of nest predation (Wilcove 1985, Wilcove et al. 1986, Yahner and Scott 1988) and brood parasitism. Tropical regions are undergoing rapid conversion from forested to open landscapes dominated by grasslands and agriculture (Gradwohl and Greenberg 1988). Areas with some of the highest rates of deforestation; the Greater Antilles, Mexico, Central America and northern South America, also have the greatest number of migrants (Terborgh 1989). Some rare and unique forest types have all but disappeared (Sader and Joyce 1988).

Many NTMB species have specialized habitat requirements which are tied to specific components within a habitat type and/or to minimum habitat areas. Due to their sensitivity to environmental changes, NTMB's function as an "early warning" system for ecosystem structure and function. An observed decline in NTMB species may herald an imminent decline in other species which depend upon similar habitat and landscape features, and will alert us to the need to take action (Sharpley-Evans 1991).

The intent of this literature review is to concentrate on those NTMB species that require a chaparral environment to successfully nest, fledge young, and find suitable food requirements. Theories of age-class and type conversion for chaparral management will also be discussed.

PHYSICAL FEATURES AND HISTORY OF CALIFORNIA CHAPARRAL

The term chaparral comes from the Spanish word "chaparro" because the early Spanish explorers were reminded of the dense shrub/oak communities found in the Mediterranean Region. Today, the term is applied to dense evergreen brushfields in general (Tyrrel 1981). The chaparral landscape is a continuous cover of low-growing shrubs with individual plants exhibiting certain diagnostic features. The plants are most easily identified by their leaves. Leaves are characteristically evergreen, small, thick, and stiff, with thick cuticles and sunken stomata (Yates 1981) in order to cope with drought conditions. Evergreen, sclerophyllous shrubs with associated ecosystems of grass, sage, scrub, broad leaved and

conifer plant communities is the dominant vegetation type in the wildlands of central and southern California, covering over one-twentieth of the State or some 13.2 million acres (Tyrrel 1981). Chaparral lands in this discussion will include predominately brush covered lands and brush-hardwood-conifer transition zones, transected by riparian vegetation.

Chaparral vegetation is the product of a "Mediterranean" climate system, characterized by moderate, moist winters with long, hot, dry summer periods. Rainfall is generally sparse (12 to 24 inches annually) and often in a few high intensity winter storms. Summer temperatures often exceed 100 degrees Fahrenheit and relative humidities are low, sometimes dropping to less than five percent (Tyrrel 1981).

Conrad (et al. 1991) states that California chaparral communities range from 500 to 3,000 feet (150 to 900 m) elevation in the north and from 1,000 to 5,000 feet (300 to 1500 m) elevation in the south. England (1990) reports that in the Grindstone, Rattlesnake, and Elk Creek drainages of the Mendocino National Forest, chamise chaparral occurs from 1200 to 4,000 feet (360 to 1220 m). On south-facing slopes, chamise chaparral gradually merges with mixed chaparral above 3,500 feet (1100 m) elevation. Mixed chaparral is the dominant vegetation on north-facing slopes from approximately 2,000 to 4,000 feet (610 to 1220 m) elevation (England 1990).

Typical chaparral species include chamise (*Adenostoma fasciculatum*), scrub oak (*Quercus dumosa*), several manzanita species (*Arctostaphylos* spp.), and several *Ceanothus* species (Table I). Growth periods for northern California chaparral species usually begin in late winter and extends through early summer when hot weather forces water conservation, decreased photosynthetic activity, and carbohydrate depletion (Conrad et al. 1991, Rundel 1981). A high percentage of chaparral is found on steep slopes. Soils vary considerably depending on topography, geology and climate prevalent in a particular area (Hanes 1973). Soils throughout the range are generally very porous, consisting mostly of sandstone and of loamy, skeletal mixed thermic composition (A. James, pers. comm). England (1990) states that there is also chaparral vegetation associated with serpentine soils on the Mendocino National Forest. Chaparral soils tend to be very low in essential plant nutrients, with nitrogen often the most limiting nutrient (Tyrrel 1981). Following fires, erosion rates can be extremely high. Often after high intensity fires a water repellent layer is produced in the soil that greatly increases runoff (Conrad et al. 1991).

Fire is a key element in the life cycle of chaparral plant species. Seasonally, the moisture content of these species can fluctuate rapidly. It is not uncommon for fuel moistures to drop to 8-13 percent during summer drought periods (Bauer 1973). Bauer (1973) also states that close spacing and continuity of vegetative cover with high surface-to-volume ratios in the chaparral community leads to a high percentage of available fuel. For example, by age 30, often as much as 50 percent of the standing mass of the crowns in a chamise stand can be dead with more dead material accumulated as litter on the ground. All of these factors result in rapid ignition and spread of fires. Where fuel conditions are uniform over broad areas, fires tend to be quite large (Tyrrel 1981).

Because chaparral evolved with fire, the vegetation developed distinct survival mechanisms. Many shrub species found in California resprout from root crowns following fire. Most species require heat treatment before the seeds will germinate and seeds can survive for extremely long periods of time in soil (Bauer 1973). The leaves of chamise contain a diverse assemblage of secondary plant compounds that play an important ecological role. Phenolic acids in the internal leaf tissues have been associated with allelopathic effects of chamise on competing species (Muller et al. 1968, McPherson and Muller 1969). A second group of chemical compounds of ecological significance are the essential oils on the

leaf surface of chamise. These volatile, high energy compounds are a very important indicator of relative flammability of the chamise. Rundel (1981) states that as post-fire succession proceeds through time there is a significant increase in the ether extractive contents of one to two year old leaf and stem tissues in chamise. This increase has been associated with the increased flammability of older stands.

Table 1 - Plant Species Associated with Chaparral

Wedgeleaf Ceanothus (<i>Ceanothus cuneatus</i>)	Blue oak (<i>Quercus douglasi</i>)
California yerba santa (<i>Eriodictyon californicum</i>)	Douglas fir (<i>Pseudotsuga menziesii</i>)
Scrub oak (<i>Quercus dumosa</i>)	Knobcone pine (<i>Pinus attenuata</i>)
Chamise (<i>Adenostoma fasciculatum</i>)	Coulter pine (<i>Pinus coulteri</i>)
Juneberry (<i>Amelanchier pallida</i>)	Sugar pine (<i>Pinus lambertiana</i>)
Fremont silktassel (<i>Garrya fremontii</i>)	Pacific madrone (<i>Arbutus menziesii</i>)
Birchleaf mountain-mahogany (<i>Cercocarpus betuloides</i>)	Tanoak (<i>Lithocarpus densiflora</i>)
Juniper (<i>Juniperus</i> spp.)	Giant chinkapin (<i>Castanopsis chrysophylla</i>)
Oak (<i>Quercus wislizeni</i> , <i>Q. chrysolepis</i> , <i>Q. vaccinifolia</i>)	Incense cedar (<i>Libocedrus decurrans</i>)
California laurel (<i>Umbellularia californica</i>)	Pacific yew (<i>Taxus brevifolia</i>)
Coyotebrush (<i>Baccharia pilularis</i> spp. <i>consanguinea</i>)	Sargent cypress (<i>Cupressus sargentii</i>)
Redbud (<i>Cercis occidentalis</i>)	Tecate cypress (<i>Cupressus forbesii</i>)
Soft chess (<i>Bromus mollis</i>)	Santa Cruz cypress (<i>Cupressus abramsiana</i>)
Cutleaf filaree (<i>Erodium cicutarium</i>)	MacNab cypress (<i>Cupressus macnabiana</i>)
Clover (<i>Trifolium</i> spp.)	Eastwood manzanita (<i>Arctostaphylos grandulosa</i>)
Pinyon pine (<i>Pinus edulis</i>)	Pinemat manzanita (<i>Arctostaphylos nevadensis</i>)
Singleleaf pinyon pine (<i>Pinus monophylla</i>)	Wartleaf ceanothus (<i>Ceanothus papillosus</i> var. <i>roweanus</i>)
Black sage (<i>Salvia mellifer</i>)	Leather oak (<i>Quercus durata</i>)
Chaparral whitethorn (<i>Ceanothus leucodermus</i>)	Chaparral current (<i>Ribes malvaceum</i> var. <i>viridifolium</i>)
Desert ceanothus (<i>Ceanothus greggii</i>)	Chaparral pea (<i>Pickeringia montana</i>)
California buckthorn (<i>Rhamnus californica</i>)	Carey balsamroot (<i>Balsamorhiza deltoidea</i>)
Deerbrush (<i>Ceanothus integrifolius</i>)	Hooker balsamroot (<i>Balsamorhiza hookeri</i>)
Hoaryleaf ceanothus (<i>Ceanothus crassifolius</i>)	Fire reedgrass (<i>Calamagrostis koeleroides</i>)
Skunkbush sumac (<i>Rhus trilobata</i>)	Houndstongue hawkweed (<i>Heiracium cynoglossoides</i> var. <i>nudicaule</i>)
Parry manzanita (<i>Arctostaphylos manzanita</i>)	Deer vetch (<i>Lotus crassifolius</i>)
Evergreen huckleberry (<i>Vaccinium ovatum</i>)	Snowy phlox (<i>Phlox speciosa</i>)
Whiteleaf manzanita (<i>Arctostaphylos viscida</i>)	Brome (<i>Bromus</i> spp.)
Greenleaf manzanita (<i>Arctostaphylos patula</i>)	Coast live oak (<i>Quercus agrifolia</i>)
Ponderosa pine (<i>Pinus ponderosa</i>)	California coffeeberry (<i>Rhamnus californica</i>)
Parry manzanita (<i>Arctostaphylos manzanita</i>)	Jeffrey pine (<i>Pinus jeffreyi</i>)
Evergreen huckleberry (<i>Vaccinium ovatum</i>)	Hollyleaf redberry (<i>Rhamnus crocea</i> var. <i>ilicifolia</i>)
Whiteleaf manzanita (<i>Arctostaphylos viscida</i>)	Redberry (<i>Rhamnus crocea</i>)
Greenleaf manzanita (<i>Arctostaphylos patula</i>)	Poison oak (<i>Toxicodendron diversilobum</i>)
Ponderosa pine (<i>Pinus ponderosa</i>)	White fir (<i>Abies concolor</i>)
California gray pine (<i>Pinus sabiniana</i>)	Deer oak (<i>Quercus sadlerian</i>)

List courtesy of Fire Effects Information System, USDA. 1992 Note: The scientific names are from the Munz taxonomic system.

While most documentation of early chaparral management consists of southern California history, it is interesting to note that in 1892 and 1893 the first forest reserves, later to become the Angeles, Cleveland, and San Bernardino National Forests, were established to protect mountain watersheds from destructive fires (Bauer 1973). These forest reserves, established by the U.S. Congress, were created in direct response to the vigorous appeals by local citizens.

In the early 1900's citizens were convinced that the fate of southern California either as an agricultural domain or metropolis resided in there liability and quality of its water supply (Tyrrel 1981). In the early 1950's, fire crews were trained to build fire breaks, fire trails, lookouts and for reforestation of burned areas, and improvement of wildlife areas. In the late 1950's the fuel break and type conversion concepts of removing chaparral and replacing it with grasses were developed and implemented in an effort to reduce fire danger and prevent erosion (Aschmann 1976).

Basically since World War II, fire suppression equipment and techniques have made improvements. Most fires today are suppressed at a few acres. Total acres burned per decade have decreased, which has resulted in older chaparral stands (Hanes 1973). All of these factors have contributed to the accumulation of more dead material which increased the fuel loading. Today, when fires occur under extreme weather conditions they are usually devastating, capable of jumping fuel breaks and highways, and destroying lives and property (Tyrrel 1981). Prescribed fire as a means of managing the age classes in chaparral now receive greater emphasis and the fuel breaks and type conversions will help accomplish the overall objectives of age class management for species diversity (Tyrrel 1981).

CHAPARRAL POST-FIRE SUCCESSION

Open stands of chaparral following fire are rapidly recolonized by the pre-fire dominants that existed before the fire. Chamise re-establishes by both resprouting from underground root crowns and by post-fire seed germination. The two other important, long-lived shrubs; wedgeleaf ceanothus and whiteleaf manzanita, are obligate reseederers (Rundel 1981). In addition to these three shrubs, four other short-lived shrub species which are generally absent from mature chamise chaparral rapidly become established following fire and form the major shrub cover for the first ten years of succession. These are California yerba santa, bush mallow (*Malacothamnus fremontii*), bush poppy (*Dendromecon rigida*), and California broom (*Lotus scoparius*) (Rundel and Lambert 1982).

Woody perennials are not the only important plant group present in the early stages of succession (Hanes 1977). Mixed herb cover also becomes rapidly established and maintains dominance in direct response to the level of total shrub cover (Rundel and Lambert 1982). Germination responses of herbaceous species has been tied to two major factors: 1) the allelopathic properties of shrubs which inhibit herb germination in the mature chaparral; 2) the stimulating effects of the burning process - heat, scarification and chemical changes. Herbs are generally inconspicuous under the mature shrub canopy (Keeley and Keeley 1981). As resprouts of chamise continue to grow rapidly in the first decade of post-fire succession, the numbers of short-lived shrubs and herbs decline rapidly (Rundel 1981). Some species such as bush mallow appear to drop out largely due to a short life cycle and lack of re-establishments of seedlings. Other short-lived shrubs and herbaceous growth appear to be shaded out since their decline in importance is inversely correlated with total shrub cover (Rundel and Lambert 1982). Chamise forms the major part of this shrub cover. Canopy closure by long-lived shrubs generally occurs by 20 years after a fire. By this stage short-lived shrubs and significant herb cover are absent from undisturbed stands of chamise chaparral (Parsons 1981).

Parsons (1981), suggests that 20 to 40 years may be a natural cycle for fire in chamise chaparral but many stands have reached considerably greater ages due to fire prevention. Wedgeleaf ceanothus, the second most dominant shrub to chamise, and an important browse plant for deer and other animals, dies out before stands reach 60 years old. Old growth chaparral has an increasing amount of dead branch tissues with age and becomes less and less productive as wildlife browse (Parsons 1981). In addition, the accumulated dead fuel makes these stands subject to high intensity fires.

SOIL AND NUTRIENT CYCLING

Considerable quantities of nutrients, particularly carbon and nitrogen, are lost through volatilization and smoke during frequent fires (DeBano and Conrad 1978). The remaining nutrients are deposited on the soil surface as ash. These post-burn nutrients are in available forms subject to export from the community by leeching or by erosion (Christensen and Muller 1975a, DeBano and Conrad 1978).

The nitrogen cycle is critical to the development of chaparral stands because chaparral soils tend to be poor in available nitrogen, and productivity of mature stands may be limited due to nitrogen deficiency. Chaparral stands receive only limited inputs of nitrogen from atmospheric sources (Hellmers et al. 1955).

Nitrogen-fixing legumes such as lupine (*Lupinus* spp.) and deerweed (*Lotus* spp.), and nonleguminous plants such as California lilac (*Ceanothus* spp.), as well as nitrogen-fixing organisms have been investigated but much remains to be learned about the dynamics of nutrients in chaparral systems (Dunn 1979, Dunn and Reynolds 1979).

After fire has swept through an area, the soil possesses a water repellent layer. The thickness and depth of the layer depends on the intensity of the fire and the nature and amount of litter present (Mishler 1978). It is thought that decomposing plant parts containing hydrophobic substances accumulate in the upper part of the soil profile (Bond 1960).

Nearly 70 percent of the long-term sedimentation from chaparral watersheds occurs during the first year after fire (Rice 1974). Fire dominates erosion and flood hydrology of chaparral watersheds. It does so by eliminating the "buffering" action of the vegetation and litter, accelerating dry ravel, increasing landslides, reducing filtration, and, most importantly, by greatly increasing peak runoff rates (DeBano and Conrad 1976).

CHAPARRAL COMMUNITIES

For the purpose of this literature review chaparral communities and their relationship with NTMB species will be referred to as chamise chaparral and mixed chaparral communities. The Wildlife Habitat Relationship (WHR) system identifies montane chaparral as a separate community. Montane chaparral occurs at high elevation and rarely intergrades with stands of chamise or mixed chaparral (England 1990). Montane chaparral will not be discussed in this literature review.

Chamise tends to dominate south-facing slopes on drier knolls and ridges from approximately 1,200 to 4,000 feet (360 to 1220 m) elevation and below approximately 2,000 feet (610 m) on north-facing slopes in the Grindstone area of the Mendocino National Forest. Buckbrush can be interspersed with chamise

on some sites. Drainages within chamise chaparral support isolated islands of chaparral oak, toyon, squawbush, and poison oak (England 1990).

England (1990) states that mixed chaparral is the dominant vegetation on north-facing slopes from approximately 2000 feet (610 m) to 4000 feet (1220 m) and on south-facing slopes from 4000 feet (1220 m) to 5000 feet (1520 m). In the Grindstone area, hillsides support a diverse mixture of scrub oak, chaparral oak, toyon, chamise, buckbrush, deerbrush, bigberry manzanita, common and whiteleaf manzanita, mountain mahogany, and interior silktassel. California bay and canyon live oak occur in small numbers throughout stands of mixed chaparral but tend to be more common in drainages. Mixed chaparral also occurs on serpentine soil where the dominant shrubs are leather oak, toyon, and *Ceanothus* species. At low elevations, mixed chaparral broadly intermingles with chamise chaparral and blue oak/gray pine woodland. At upper elevations it borders yellow pine and mixed conifer forest. Small stands of knobcone pine occur at scattered locations within mixed chaparral on north and east-facing slopes (England 1990).

Chamise and mixed chaparral can intergrade over large areas. Distinguishing between these types is a subjective interpretation usually based on percent cover of chamise. Chamise chaparral may consist of nearly pure stands of chamise or may be in conjunction with other shrubs (Cheatham and Haller 1975, Thorne 1976, Hanes 1977). The purest stands occur on xeric, south-facing slopes in southern California (Hanes 1976). Payson et al. (1980), classifies chaparral as chamise if it is the "dominant" species. Hanes (1977) considers a stand chamise when it comprises 50-100 percent of total cover.

An important floristic component in chamise chaparral is the riparian inclusions. Within large relatively xeric areas dominated by chamise chaparral are isolated patches of more mesic vegetation along drainages (England 1988b). Similarly, in mixed chaparral on north-facing slopes, vegetation along drainages can be dominated by California bay and canyon live oak. Patches generally cover a relatively small area but are of great importance to several NTMB species that were found to be exclusively in these islands, especially in very young stands of chamise (England 1988a). These inclusions are caused by local differences in soil moisture conditions, and the patches are too small to warrant identification as a different stand type (England 1990).

MANAGING CHAPARRAL FOR WILDLIFE

Chaparral management techniques affect wildlife and wildlife habitat (Quinn 1979). The abundance and diversity of wildlife in chaparral is not commonly recognized. During a 2 year period on the San Dimas Experimental Forest in southern California, chaparral habitat was found to support 49 mammal species and 85 species of birds with the majority of birds being at the mid-elevational range of 3000 to 4200 feet (900 to 1300 m) (Quinn 1981, Wirtz 1979). Flower-attracted insects, especially bees, are more abundant and species-rich in chaparral than in any other California vegetation and are responsible for most pollination (Force 1979).

Fire in chaparral can profoundly affect the structure and composition of the plant and animal community (Wirtz 1977). These changes in the plant and animal communities are normally temporary, however, over time, chamise has the capability to dominate over relatively short-lived shrubs such as *Ceanothus* due to its rapid regeneration from seed and root-crown sprouts (England 1990). It is of value to know the fluctuation patterns of various animal communities as they relate to the fire cycle and to plant succession. It is also of value to know how fire frequency, intensity and size directly affects animal communities (Quinn 1979).

Wirtz (1977) found both bird species richness and diversity increased during 42 months post-fire in southern California chaparral. An increase number of species present in higher elevation burned areas in the first spring post-fire may reflect increased richness in both insect and plant food resources associated with spring growth. While increases were noticed in seed/insect feeding bird species, insect/fruit feeding species exhibited an initial decrease until fruits became available in the second spring post-fire. Species that glean insects from vegetation also exhibited an initial decrease in utilization of burned areas, however, those species that take insects from the air appeared unaffected (Wirtz 1977).

For the Mendocino National Forest, England (1990) concluded the following from literature and personal observations the following:

- 1) Avian species richness and density increase for several years after a fire, then decline as shrub cover increases and the vegetation becomes decadent.
- 2) Avian species with grassland affinities are most abundant for several years after fire.
- 3) Edge effects between burns of different ages are an important influence on community structure.
- 4) Granivorous birds dominate the avifauna during the winter and insectivorous birds are much more common in spring.

Atkins (1977), and Cody et al. (1977) reported seasonal changes in biomass and diversity of chaparral insects in southern California. Diversity for the total insect fauna peaked in May; its lowest point was in October. Atkins (1977) then divided the herbivores into sap feeders and foliage feeders. Foliage feeders were more diverse for the first six months of the year, the sap feeders were more diverse the remaining six months. He found the greatest diversity in April and May, corresponding with plant growth and a preponderance of flowering, and another unexplained peak in August (Atkins 1977).

Force (1979) found that plant species richness is greater after a burn than in later years as chaparral succession proceeds to maturity. A large number of "fire annuals" or annual plants grow from seeds which have been lying dormant in the ground until stimulated by fire to germinate. They develop rapidly and form a thick ground cover for perhaps two years. Another group of plants present after fire is the suffrutescents that live for three to seven years (Moldenke 1976). Because the variety and abundance of flower-visiting insects might reasonably be expected to relate to floral variety and abundance, then one might expect nearly twice as many flower-visiting insect species in burned chaparral as in mature chaparral (Moldenke 1976). Wirtz (1979) states in early years after fire these insects are sufficiently abundant to constitute an important food resource for birds. Of the 55 species of birds in chaparral he identified, 35 belonged to guilds that feed largely or exclusively upon insects.

Type conversion of chaparral to grasslands has been practiced in California since the late 1950's for the purpose of wildlife habitat improvement, fire control, increased water yield, and improved grasslands for cattle grazing (Rosario and Lathrop 1967). Conversion is accomplished through brush removal by mechanical means, in some cases, crushing, herbicide treatment and disking, before the re-planting of perennial grass seed (England 1986). Research conducted on Arizona rangelands show that type conversion through prescribed fire, in an attempt to improve forage supply for grazing animals, must be conducted at least every 10 years for continued sustainment (Bolander 1981).

Attempts have been made to convert California chaparral to forest. Many of these plantings have failed. The trees able to tolerate drought conditions and poor soil, were often killed by the frequent wildfires of this region (Radtke et al. 1981).

Native American groups throughout California have used fire as a tool to manipulate their environment. Early successional plant types were beneficial for increased forage for game animals as well as providing food and resources for themselves (Lewis 1973). Burning may have been carried out to increase ecotones, which are generally more productive than other areas. Native American population densities were larger in northern California than southern California, therefore burning activity was probably more intense in northern California. In areas of high population densities Native Americans influenced the floral and faunal make-up of large landscapes, including chaparral, over thousands of years (Lewis 1973).

There is much to be learned of the effects of fires of various intensities and frequencies, taking place during various seasons of the year, have on the ecosystem (Hunter 1981). Shea et al. (1981) believes that it is highly improbable that periodic low intensity burning in spring duplicates the "natural" fire regime. Low-intensity spring burning is disfavorable as heat penetration is not sufficient to stimulate seed germination in the soil. VanWilgen (in press) shows that initially spring burning was encouraged as being less hazardous with regard to erosion; today, burning between the end of April and the end of August is strongly discouraged. Burning between the end of February and the end of April is recommended and the intention is to limit spring burning only to cases where safety and the work load make them unavoidable.

Current information suggests that, in general, wildlife habitat may be optimized by maintaining chaparral in many age classes through rotational prescribed burning. While more studies need to be conducted per geographical location regarding the optimal time of year to burn, information shows that erosion can be better controlled if conducted after annual rains. In contrast if soil moisture is high, low fire intensity may not insure that seed germination takes place. Studies also show that both insect and avian species richness and diversity increase for several years after a fire. Type conversion of shrublands to grasslands encourages avian diversity and attracts those species with grassland affinities, however, requires more frequent treatment for continued sustainment.

FRAGMENTATION

Extensive research in North America has shown that the presence of migratory birds breeding in temperate forests is intricately related to tract size (Whitcomb et al. 1981, Lynch and Whigham 1984, Blake and Karr 1987, Robbins et al. 1989). When a large, continuous tract of a vegetation type is converted to other vegetation types only scattered fragments of the original vegetation type remains (Faaborg et al. 1993). These fragments occupy less area and are separated by habitats different than the original vegetation type.

Fire is one method that creates sharp ecotone edge in place of the natural soft mosaic of vegetation transition. This "edge effect" is a junction of two dissimilar habitat types (Faaborg et al. 1993). The results of increased forest fragmentation, resulting in greater edge effect, can negatively effect NTMB species in relationship to overall interior size of habitat (Finch 1991b). Studies show that greater nest predation and brood parasitism takes place in small vegetation fragments than in large interior tracts (Faaborg et al. 1993). Predation and brood parasitism is also greater near the edge of large habitat areas than in the interior (Wilcove 1985).

It was once thought that the creation of edge was beneficial to migratory birds, however, it has been found that many species require extensive areas of unfragmented habitat (Finch 1991b). Species which nest close to or on the ground are especially vulnerable to nest predation at habitat edges (Wilcove 1985). Robinson et al. (1993) states that brood parasitism by brown-headed cowbirds appears to also be higher near forest edges where the ecotone is produced by a field-forest edge. Higher densities of nests along the forest edge, as observed by Gates and Gysel (1978), may result in increased predator densities or predator search effort.

Forest fragment size and shape appears to be significant in the breeding success of NTMB species, where shapes that maximize core areas are preferred to narrow shapes that maximize edge effects (Faaborg et al. 1993). Diamond (1975) states that one large fragment is superior to many small fragments, and several fragments close together are superior to several fragments far apart. In chaparral, studies show that edge effects between burns of different ages have an important influence on community structure (Lawrence 1966, Bell 1974, Nelson 1975, Longhurst 1978). Faaborg et al. (1993) suggests that although small fragments may not provide breeding habitat for most area sensitive birds, they may provide stop-over and foraging sites during migration, provide breeding habitat for short distance migrants and permanent residents, and may support non-breeding populations of Neotropical migrants.

NEOTROPICAL MIGRATORY BIRDS IN CHAPARRAL

Table 2 contains a list of NTMB species which migrate from south of the continental U.S. to northern temperate zones of chaparral on the Mendocino National Forest, for the specific purpose of breeding, nesting, and fledging young. The list is obtained from personal observations of England (1990), whose study areas include the Grindstone, Rattlesnake, and Elk Creek drainages on the eastern slopes of the North Coast Range in western Glenn County, California. A few sites were also selected near Fouts Spring in extreme northwestern Colusa County and near Paskenta in southwestern Tehama County. Excluded are those species which winter within the continental U.S., are yearlong residents, or which utilize chaparral solely for foraging. Migration verification for the species listed is by Peterson (1969), Verner and Boss (1980), and Udvardy (1977).

Table 2

Common Poorwill (<i>Phalaenoptilus nuttallii</i>)	Nashville Warbler (<i>Vermivora ruficapilla</i>)
White-throated Swift (<i>Aeronautes saxatalis</i>)	Yellow Warbler (<i>Dendroica petechia</i>)
Calliope Hummingbird (<i>Stellula calliope</i>)	Black-throated Gray Warbler (<i>Dendroica nigrescens</i>)
Rufous Hummingbird (<i>Selasphorus rufus</i>)	MacGillivray's Warbler (<i>Oporornis tolmiei</i>)
Allen's Hummingbird (<i>Selasphorus sasin</i>)	Wilson's Warbler (<i>Wilsonia pusilla</i>)
Western Wood Peewee (<i>Contopus sordidulus</i>)	Western Tanager (<i>Piranga ludoviciana</i>)
Dusky Flycatcher (<i>Empidonax oberholseri</i>)	Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)
Western (or Pacific Slope) Flycatcher (<i>Empidonax difficilis</i>)	Lazuli Bunting (<i>Passerina amoena</i>)
Ash-throated Flycatcher (<i>Myiarchus cinerascens</i>)	Chipping Sparrow (<i>Spizella passerina</i>)
Western Kingbird (<i>Tyrannus verticalis</i>)	Dark-eyed (or Slate-colored) Junco (<i>Junco hyemalis</i>)
Cliff Swallow (<i>Hirundo pyrrhonota</i>)	
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	
Solitary Vireo (<i>Vireo solitarius</i>)	

Birds are extremely mobile and range widely over many habitat types, but only specific types are chosen for breeding or foraging (Cody 1985a). The ability to obtain food and shelter determines their habitat of preference. Structural features of landscapes and presence of other species may also be a deciding factor. Studies have demonstrated a strong correlation between vegetative structure and specific bird species (Sherry and Holmes 1985). Foliage height diversity has been shown to be an important structural component where bird species richness and diversity may vary in correlation to layers of vegetation (MacArthur and MacArthur 1961). When a particular habitat offers multi-layered foliage, those with more vertically even layers support the greatest species diversity (Cody 1985b). Also, microclimate features such as; nest placement to avoid excessive wind, excessive diurnal heat, and concealment from predators, can determine nesting success (Walsberg 1985, Shuford 1993).

There is little comparable information available regarding migratory birds in chaparral and their specific placement within habitats. In England's (1990) evaluation, site preference is based on habitat (chamise or mixed chaparral), canopy cover (classified as dense, moderate, open or sparse), and age class (measured by crown decadence as; seedling, young, mature and decadent). Table 3 shows the migrant species habitat placement expected according to reference, and actual habitats utilized by individual species observed on the Mendocino National Forest.

Table 3

Parulidae comprises the wood warblers, small, very active, brightly colored birds. They have slender, straight, pointed bills. Warblers are almost entirely insectivores (Robbins et al. 1966).

Common Name	Habitat Requirement
Nashville Warbler	An uncommon to common summer resident in California. Most common breeding habitat includes ponderosa pine, montane hardwood-conifer, mixed conifer, and montane chaparral (Zeiner et al. 1990). Finds cover in oak and coniferous forests with shrub understories and ground vegetation. Edge areas important for foraging (Timossi 1990). Observed single individuals to not use chamise, solely in mixed chaparral with dense cover in all age classes but seedling (England 1990).
Yellow Warbler	Uncommon to common residents in northern California. Breeds in riparian woodlands of montane chaparral and in open ponderosa pine and mixed conifer habitat with substantial shrub cover (Grinnell and Miller 1944, Zeiner et al. 1990). Uses a wide variety of vegetation as cover, frequently in riparian inclusions, which is important also for nesting and foraging (Smyth and Coulombe 1971). Observed in both chamise and mixed chaparral in low abundance with the majority of birds in dense chamise of mature and young age class (England 1990).

**Black-throated
Gray Warbler**

Fairly common summer breeding resident in northern California. Most common breeding habitat includes ponderosa pine, valley foothill-hardwood conifer, montane hardwood, and pinon-juniper areas (Zeiner et al. 1990). Utilizes cover provided by brushy understory and trees of oak woodland. Shows preference for sites with low percentage canopy cover (Verner and Boss 1980). Observed in both chamise and mixed chaparral in dense, mature to decadent age classes (England 1990).

**MacGillivray
Warbler**

Summer residents in moist habitats with dense brush. Preferred habitat includes valley foothill riparian vegetation (Zeiner et al. 1990). Seeks cover for breeding and feeding in willows, alders and dense shrubs in riparian areas. Successional brush fields near water also used for nesting (Zeiner et al. 1990). Observed using islands of oak/toyon/manzanita along drainages. Found in both chamise and mixed chaparral in low numbers in dense cover (England 1990).

**Orange-crowned
Warbler**

Some birds remain in California for the winter, but most leave northern California by mid-October (Timossi 1990). Most common breeding habitat includes chaparral, valley foothill hardwood, blue oak and riparian areas (Zeiner et al. 1990). Utilizes the cover of chaparral, brushy stages of woodlands, forests and riparian habitats. Requires dense brush for nesting (Verner and Boss 1980). Observed in both chamise and mixed chaparral in oak/toyon/manzanita islands. Numbers decrease with increasing shrub cover (England 1990.)

**Wilson's
Warbler**

Common spring and summer migrants in almost all woodland and shrub area on the coast and in the interior of California (DeSante and Ainley 1980). Willows, alders, and shrub tickets and areas of cover for these birds. Beedy (1975) reports foraging along forest edges and within dense coniferous forests. Observed in both chamise and mixed chaparral, spring through fall in chamise, and spring abundance in moderate and dense cover classes, absent elsewhere (England 1990).

Grosbeaks, finches, sparrows, and buntings make up the family of *Fringillidae*. The obvious feature of this family is the bill which is short and stout, for seed-cracking. Many species are highly colored; the sparrows are brown streaked. Their main food source is seeds, insects and small fruits (Peterson 1969).

Common Name

Habitat Requirement

**Black-headed
Grosbeak**

Commonly a spring and summer inhabitant of southern California. This species frequents valley foothill hardwoods, conifer and riparian (Zeiner et al. 1990). Usually nests in deciduous trees and bushes bordering streams (Weston 1947), or wooded sites with low canopy streams (Weston 1969). Observed to be uncommon with higher occurrence in open, mixed chaparral than chamise (England 1990).

Lazuli Bunting

Breeds in arid brushy canyons, riparian thickets, chaparral, and open woodlands (Ehrlich et al. 1988). Frequently are found in brushy understories of wooded habitat. Observed as an uncommon spring and summer resident. Generally higher abundance in both chamise and mixed chaparral than shown in the WHR, the majority in dense and moderate cover (England 1990).

Chipping Sparrow

Found more commonly in montane habitats, northern coastal ranges and the Great Basin, than in southern and interior foothills (McCakie et al. 1988, Zeiner et al. 1990). Found in many habitat types, from chaparral to lodgepole pine forests with canopy closure less than 40% percent (Timossi 1990). WHR lists this species as a yearlong resident, but England (1990) finds no sitings till May. An uncommon summer-spring resident, only two birds have been observed, both in a dense, mature stands of chamise. Nests in conifers but may also use deciduous trees, shrubs, or vines (Grinnell and Miller 1944).

Dark-eye Junco

Portions of the population remain in California over winter while others migrate to Mexico. England (1990) reports this species as an uncommon winter resident. No detections were made in riparian inclusions. Low abundance in all age classes of chamise. Higher abundance in young, dense mixed chaparral. Terres (1980) found that species are most often found at forest and woodland edges; avoids deep forest interiors.

Male tanagers (*Thraupidae*) are brilliantly colored, with the western species exhibiting bright red. Females are greenish above, and yellow below, suggesting large warblers or vireos. Their shorter, thicker beaks are usually notched or "toothed". Insects and small fruit are their main food source (Peterson 1969).

Common Name	Habitat Requirement
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Western Tanager

During the breeding season, they prefer moderately open mature coniferous forests with associated hardwoods. Use trees and shrubs for nesting, roosting, and other cover (Zeiner et al. 1990). England (1990) observed 28 birds between April and June in both chamise and mixed chaparral. Approximately 67 percent of those using chamise chaparral were using oak/toyon/manzanita islands along drainages. Majority of birds found in dense to moderate cover, with 8 sitings in seedlings age class.

Flycatchers (*Tyrannidae*) usually perch quietly on exposed branches waiting to snap up passing insects. Bills are rather flattened, with bristles at the base of most species. Insects are their main food source, with some species eating fruit and small reptiles (Peterson 1969).

Common Name	Habitat Requirement
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Western Kingbird

Inhabits areas of open lowlands, grasslands and croplands bordered by trees of low to medium canopy cover. Shrubs and woodland habitats which are sparse and open are also used (Grinnell and Miller 1944). Oak, Cottonwood, or willow are the species most commonly used for nesting (Ehrlich et al. 1988.) England (1990) observed 30 birds between April and June in both chamise and mixed chaparral. In chamise, birds preferred seedling age class. In mixed chaparral most were found in mature, dense to moderate cover habitat.

Ash-throated Flycatcher	Prefers nesting in scrub, chaparral, open oak and riparian woodlands (Zeiner et al. 1990). This species forages over low shrubbery. Water does not seem to be an important habitat requirement (Williams and Koenig 1980). Observed in both chamise and mixed chaparral in all age class and cover types. This species is a fairly common breeding season resident (England 1990).
Pacific-Slope Flycatcher	A fairly common summer resident in warm, damp woodlands including closed-cone pine-cypress and ponderosa pine habitats (Zeiner et al. 1990). Typically found in areas that are well shaded by tall trees and/or steep canyon walls (Grinnell and Miller 1944). A single bird was observed in a decadent stand of mixed chaparral with dense shrub cover in May (England 1990).
Dusky Flycatcher	Lives in deciduous, or coniferous habitat of mixed brushlands and trees, situated near forest edges. Essential cover elements are low growing thickets for nesting and foraging (Verner and Boss 1980). Also requires adjacent, high singing/look-out posts. Nests are commonly found on a forest edge, near shrubby areas, and clearings (Ehrlich et al. 1988). England (1990) observed 30 birds between April and July in both chamise and mixed chaparral in dense mature cover. They are thought to breed in ponderosa/blue oak woodlands edges and forage over chaparral.
Western Wood Peewee	Most common in open woodlands and forests with sparse, to moderate canopy, which edge on meadows, streams, lakes, and other moist, open habitats (DeGraaf et al. 1991). Requires trees with dead tops or exposed branches for unobstructed views and singing posts (Kilgore 1971). Observed in both habitat types and age classes from April to June. Seems to prefer dense mature to decadent age class although 8 sightings were in young and seedling age classes (England 1990).

Hummingbirds, the smallest of all birds, are found in the family *Trochilidae*. Usually iridescent, they have needle-like beaks for sipping nectar from flowers. They will hover when feeding and the wing motion is so rapid that the wings are blurred, making identification difficult (Peterson 1969).

Common Name	Habitat Requirement
Calliope Hummingbird	Smallest of the hummingbird species. Breeds in deciduous and/or coniferous open woodlands in canyon bottoms, valley floors and forest glades. Forest edges adjacent to meadows and shrublands are also favorable (Johnsgard 1983). Nests are frequently placed in conifers, within close proximity to water (Weydemeyer 1927). Four observations of this species were made in April and May. Three of the birds were found in chamise chaparral, two in seedling stands and one in a mature dense stand. The fourth was in a dense decadent stand of mixed chaparral (England 1990).

**Rufous
Hummingbird**

There is no confirmed nesting requirements for California. Further north (Oregon) they nest in coniferous forests, thickets and brushy slopes, often foraging in adjacent meadows (Johnsgard 1983). Other nesting sites include huckleberry bushes, alders, and blackberry vines (Johnsgard 1983). England (1990) observed eight adult males in April and May, with the majority being in dense chamise of all age classes.

**Allen's
Hummingbird**

Prefer streamside thickets with a sparse to open canopy closure but very dense growth of understory shrubs (Johnsgard 1983). Shade is an important consideration when nest building, in oaks, willows, tangles and thickets (Aldrich 1945). Only a single adult male has been observed, which was in July. He was sighted in a young stand of chamise chaparral with moderate cover (England 1990).

Poorwills are in the family *Caprimulgidae*. They are nocturnal birds with ample tails, large eyes, tiny bills, huge gapes, and very short legs. During the day they rest horizontally on a limb or on the ground, camouflaged by "dead leaf" pattern. They forage mainly on nocturnal insects (Peterson 1969).

Common Name	Habitat Requirement
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**Common
Poorwill**

Are known to utilize chamise chaparral for cover and foraging (Timossi 1990). Breed in open areas, prairies, hillsides, or scattered brush of semi-arid regions (Harrison 1978). Nests are located close to wood debris or vegetation, often partially shaded by a bush or shrub (Aldrich 1935). Ten birds were observed, nine between April and July and one in February. All but one siting was in chamise chaparral, in stands with dense shrub cover (England 1990).

Swallows (*Hirundinidae*) are slim, streamlined birds with graceful flight characteristics. Sparrow sized birds, they have tiny feet, long pointed wings, and short bills with very large gapes. Food source consists of flying insects and occasionally berries (Peterson 1969).

Common Name	Habitat Requirement
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Cliff Swallow

Habitat is generally open country, where they frequent meadows, shrublands, grasslands and pasture (Zeiner et al. 1990). Nests are built under the eaves of bridges, buildings, or highway culverts. England (1990) observed 12 flocks of 1 to 75 birds foraging over both chamise and mixed chaparral in May and June. All observations were within 3-10 km of a highway where this species nested in cement culverts. Must have mud available for nest building (Zeiner et al. 1990).

Swifts belong to the *Apodidae* family and are swallow-like in appearance. They have slim scythelike wings and short tails. They are structurally distinct, with flat skulls and all four toes pointing forward. Flight is very rapid, sailing between spurts (Peterson 1969).

Common Name Habitat Requirement

White-throated Swift Nest in mountainous country near cliffs and canyons. Nest is placed in a deep crevice in the face of rocky cliffs usually high above the ground (Grinnell and Miller 1944). Are spring and summer residents of the Mendocino N.F., but are residents in southern California (Timossi 1990). England (1990) observed single individuals foraging over chamise chaparral. Swifts are not known to spend any time on the ground (Bartholomew et al. 1937).

Gnatcatchers (*Sylviidae*) are tiny, active birds with small slender bills. They have long mobile tails and feed on mainly insects, insect eggs, and larvae (Peterson 1969).

Common Name Habitat Requirement

Blue-gray Gnatcatcher Nests in open woodlands or where scattered trees (especially oaks), are interspersed with chaparral or sagebrush. Requires canopy closure to be less than 40 percent for nesting (Ehlrich et al. 1988). Nest is built near the top of a live tree or shrub, usually within 25 feet off the ground. England (1990) states that they are found in both chamise and mixed chaparral in low abundance and are an uncommon spring-summer resident.

Vireos (*Vireonidae*) are small olive or gray-backed birds, much like wood warblers, but with somewhat heavier bills. They are less active than warblers, and search for insects under leaves. They may be divided into two groups; one with wing bars and one without (Peterson 1969).

Common Name Habitat Requirement

Solitary Vireo A woodland species, frequents the middle levels of trees, whether conifers, oaks, or other broadleafed trees. Nests are built in a horizontal V-shaped fork and are placed in shrubs or trees with apparently no strong preference for a particular species of plant (Terres 1980). England (1990) observed seven adult males in June. All birds were in mature stands of mixed chaparral with dense shrub cover. All sites were associated with canyon live oak.

FACTORS INFLUENCING SUCCESSFUL NEST PLACEMENT

Birds are particularly responsive to changes in the physical structure of habitats in which they chose to nest and forage (Cody 1985a). In chaparral habitat, riparian areas are of great concern because of the extraordinary wildlife value (England 1990). Birds are vulnerable to disturbance and fragmentation associated with livestock grazing, agriculture, water management, timber harvest, recreation, urbanization, and other land use activities (Thomas et al. 1979, Knopf et al. 1988).

Livestock potentially have their greatest impact on birds where grazing has changed the physical structure of habitat. Cattle compact soil, remove plant materials, and indirectly reduce water filtration, which results in decreased vegetation density (Holechek et al. 1989). Certain foraging and nesting guilds have been affected by grazing more than others. The open-nesting birds are significantly

influenced as well as those species that feed on nectar, insects, or seeds in the understory or on the ground (Sedgewick and Knopf 1987). Most neotropical migrants negatively impacted by livestock grazing are species that nest and/or forage in heavy shrub or herbaceous ground cover, and/or that may be vulnerable to brown-headed cowbird (*Molothrus ater*) parasitism (Knopf et al. 1988).

Of the ten families observed in chaparral habitat on the Mendocino National Forest (England 1990), studies show that three families are negatively affected by livestock grazing (Knopf et al. 1988):

Warblers (*Parulidae*), specifically:

MacGillivray's Warbler
Wilson's Warbler
Yellow Warbler

Sparrow/Junco (*Fringillidae*), specifically:

Chipping Sparrow
Dark-eyed Junco

Hummingbird (*Trochilidae*), specifically:

Calliope Hummingbird

Table 4 illustrates nest design and physical description of nest placement for those migratory species that utilize chaparral habitats on the Mendocino National Forest (England 1990). The cliff swallow will be omitted from this table as their nest has been shown to be adjacent to chaparral, in mud colonies constructed in cement highway culverts. Nesting information provided by Verner and Boss (1980). Nest height is measured in feet (').

Table 4

Common Name	Nest Design	Description
Nashville Warbler	open cup	May to July, nests on ground in dense shrubs and sparse trees.
Yellow Warbler	open cup	April to July, nests in low bushes in riparian sites. Height from ground, 2' to 12'.
Black-throated Gray Warbler	open cup	May to July, nests on horizontal branch usually 3' to 10' above ground.
MacGillivray's Warbler	open cup	May to July, nests usually 2' to 6' above ground in shrubs of riparian type associated with tall grasses and herbs.
Orange-crowned Warbler	open cup	April to June, nests on ground or less than 3' from ground in a low, dense bush.
Wilson's Warbler	open cup	April to July, nests on ground among mosses and grasses, at base of low dense shrub.
Black-headed Grosbeak	open cup	April to August, nests in shrub or deciduous tree, near water usually 6' to 12' above ground.
Lazuli Bunting	open cup	March to August, nests in thick, low vegetation of riparian sites, 1.5' to 4' above ground.
Chipping Sparrow	open cup	April to July, nests near outer end of branch, usually of conifer, from 5' to 40' above ground.
Dark-eyed Junco	open cup	May to August, nests on ground, near water, concealed beneath grasses, shrubs, fallen logs.
Western Tanager	open cup	May to August, nests toward end of horizontal branch, 6' to 50' above ground.

Common Name	Nest Design	Description
Western Kingbird	open cup	April to July, nests on a horizontal branch of oak, willow, or cottonwood, from 15' to 30' above ground.
Ash-throated Flycatcher	cavity	April to June, nests in knot holes of oaks, cottonwoods, old stumps, sometimes 20' up.
Pacific-Slope Flycatcher	cavity	May to July, nests in crotch of oaks with dense canopy cover, near water.
Dusky Flycatcher	open cup	May to July, nests attached to low twigs in shrubs or trees in dry sites. From 4' to 6' above ground.
Western Wood Peewee	open cup	May to August, nests in fork or horizontal branch in tree of any species, 10' to 50' above ground.
Calliope Hummingbird	open cup	May to July, nests below live branches of lodgepole pine, in riparian sties, from 10' to 30' above ground.
Rufous Hummingbird	open cup	No confirmed nesting information for California. Nests on brushy slopes, in conifers and thickets in Oregon.
Allen's Hummingbird	open cup	Found in open sites, from gray pine-oak wood lands up. No confirmed nesting requirement for California.
Common Poorwill	scrape	March to August, nests in scrape on ground matted with pine needles, next to a log and concealed by shrubs.
White-throated Swift	crevices	May to August, nests in deep crevice in steep, rocky cliff face, from 10' to 200' or more above base of cliff.
Blue-gray Gnatcatcher	open cup	April to August, nests in live tree or shrub, usually near top, in fork between two branches, 3' to 45' up.
Solitary Vireo	open cup	April to July, nests usually in low, dense foliage of shaded shrub, 5' to 20' up.

While studies show negative impacts of livestock grazing on three families of migratory birds that utilize chaparral (Knopf et al. 1988), there are similarities for other species as well. Grazing may impact those species that nest on or close to the ground, require dense low foliage for cover, and forage in understory or on the ground. Of 24 species listed, all but four construct open cup nests. Studies also show increased cowbird parasitism when foliage is denuded (Knopf et al. 1988). Riparian habitat is utilized directly by eight species and others are also influenced by the presence of water when searching for optimum nesting sites. Further studies need to be conducted specifically for chaparral migrants, to discover species diversity and use, and to monitor the impacts of livestock grazing and other land uses practices.

Populations of brown-headed cowbirds have increased to the point where they pose a potential threat to populations of many neotropical migrant songbirds (Mayfield 1977, Brittingham and Temple 1983). The brown-headed cowbird is a generalist brood parasite that lays its eggs in the nests of over 240 known host species, the majority of which are neotropical migrants (Friedmann and Kiff 1985).

Historically, cowbirds were largely confined to mid-continental prairies where they presumably followed herds of nomadic bison. Cowbirds mainly search for seeds and insects in short grass and on bare ground and may have depended on grazing by large ungulates to create suitable feeding conditions (Mayfield 1965). Cowbirds have extended their geographical range westward as new feeding areas became available, with the widespread introduction of livestock (Robbins et al. 1986).

Increasing cowbird populations pose a potential threat to many hosts because of the cowbird's extraordinary fecundity and the extent to which cowbird parasitism reduces host productivity. Female cowbirds lay an average of 30 to 40 eggs per season (Rothstein et al. 1986). Relatively small numbers of cowbirds can therefore parasitize many nests. Friedmann (1963) and Roskoff et al. (1990) stated that cowbird parasitism reduces host productivity for the following reasons:

- 1) Female cowbirds remove host eggs (usually one) from 33% to 90% of all parasitized nests.
- 2) Cowbird eggs are unusually thick and, when laid, often break those of the host.
- 3) Cowbird eggs have a short incubation period of 11 days compared with 12-14 days for most hosts.
- 4) Cowbirds usually parasitize hosts smaller than themselves, which gives cowbird nestlings a further advantage in competition with host young.
- 5) Cowbird nestlings grow faster, beg more loudly, and have wider gapes than host nestlings.

As a result, small hosts species with long incubations periods usually fail to produce any of their own young if a single cowbird egg hatches (Rothstein 1975).

Neotropical migrants are especially vulnerable to cowbird parasitism. Most neotropical migrants build open-cup nests, which are the most frequent target of cowbirds (Friedmann 1929). The cowbird egg-laying period generally extends from mid-April to mid-July, which also coincides with the major period of egg-laying in most neotropical migrants (Whitcomb et al. 1981).

Cowbirds tend to be most abundant in heterogeneous "fragmented" landscapes in which grassy areas are intermixed with shrubby old fields and/or forests (Rothstein et al. 1986). They are also associated with edges between habitat types, pastures, recently plowed fields and livestock feeding yards. Within a site, the percentage of nests parasitized can vary with the structure of the vegetation. Cowbirds are frequently perched or displaying at the top of dead snags to locate potential host nests and observe host behavior (Freeman et al. 1990).

Cowbird hosts with restricted geographical ranges can be particularly vulnerable to parasitism. Cowbird parasitism is considered one major cause (along with habitat loss) of population declines and endangered status of many migratory species (Grzybowski et al. 1986).

Information is lacking concerning the level of impact of cowbird parasitism in northern California chaparral communities. However, Udvardy (1977) suggests that warblers, finches, and vireos are the favorite hosts of cowbirds, and that some warbler populations are in danger from such pressure. For example, if a female yellow warbler discovers a cowbird parasitizing her nest, she quickly covers the alien egg with another foundation and lays another clutch. One nest was found to be five layers deep (Udvardy 1977).

FORAGING MANEUVERS

Martin and Karr (1990) observed that changes in available food types and in food demands relative to availability, effect the plasticity of some species foraging maneuvers. Many elevational migratory species are insectivores only seasonally, feeding on seeds and fruit in winter. Atkins (1977) and Cody et

al. (1977) reported seasonal changes in biomass and diversity of chaparral insects in southern California. As might be expected from seasonal and productivity data, the biomass of chaparral insects (for 1973) was greatest in the spring (Mooney et al. 1977). Naturally this productivity sequence of insects has a tremendous effect on vertebrate insectivores (Cody et al. 1977).

In chaparral habitat the greatest diversity of insects occurs at the end of March. A second peak, much lower than the first, occurred in May, with an overall gradual decrease to the end of the year with the lowest diversity occurring in January (Cody et al. 1977). This pattern was undoubtedly influenced by the temperature and rainfall pattern and the vegetational response to these factors. Foliage would naturally be more abundant and succulent during and immediately after the rainy season. Foliage-dependant arthropods and their density on the substrate increase through spring, and decrease in the fall (Atkins 1977). Sap might be somewhat less available in the dry season than in the wet, but it should provide nutrition in addition to being a source of moisture when free water is scarce.

Cody (1974) reported flying insect catches from both north and south slope chaparral in southern California in a 1968-69 census. The biomass from the north slope tended to peak later in the season and was greater overall than that from the south slope. He found a corresponding higher percentage of the insectivorous birds on the north slope than the south. Cody and Mooney (1978) also describe a chaparral vertical density profile associated with corresponding profiles for insect density and bird utilization. Insect densities appeared to be greatest at about 1.5 m above the ground, which is also the level where vegetation density and bird insectivore activity were greatest.

In discussing seasonal timing of migration, the important determining factors are, the vegetational development in spring, food availability, and climatic factors in spring and fall (Weydemeyer 1973). In a 48 year study of spring arrivals of migrants in Montana, Weydemeyer (1973) found ranges in dates of arrival were greatest for species arriving late March and April and least for species arriving late May and June. Pinkowski and Bajorek (1976) concluded that granivorous, omnivorous, and aquatic species tend to arrive earlier than strictly insectivorous species, and earlier arriving species have a greater variance in arrival time than species arriving late in spring.

Changes in distribution of migrants among habitat types from one migratory season to the next are consistent with en-route habitat selection (Hutto 1985). For example, foliage-gleaning, insectivorous migrants showed shifts in habitats used from one migratory season to the next during passage through southeastern Arizona. Changes were tied to changes in insect availability. En-route habitat selection occurs because the probability a migrant will meet its energetic requirements and achieve safe passage is directly correlated with the intrinsic suitability of stopover habitat (Moore and Simons 1992). The physical structure of habitat, including plant species composition and foliage structure, influences habitat selection and how they see and capture prey (Holmes and Robinson 1981). Such constraints could effect rates at which migrants replenish energy reserves following migration.

What cues migrants use to select among alternative habitats is poorly understood (Finch 1991b). Each species is restricted in its habitat by various physiological and morphological traits that govern foraging behavior, and can exist only if their requirements are met (Balda 1975). While some species are able to function within a narrow range of factors, others have a broad range of tolerance for feeding requisites. Key factors that determine foraging patterns of birds are; foraging height, foraging location within the canopy, and the preferential use of tree/shrub species or other foraging substrates (Anderson 1980).

In chaparral habitats, one possible reason for decreased insect density in the fall is the lowered protein content in new buds and young growing leaf tissue over the summer growing season (Feeny 1970). By late summer, protein content is below 30% in leaf tissue that has matured. In chaparral soils where nitrogen is deficient, this may be one of the most important governing factors of low productivity in mature stands of chamise and mixed chaparral, which correlates with decreasing arthropod density in fall (Hellmers et al. 1955).

Table 5 represents each bird species (England 1990), their foraging classification and methods of obtaining food, in chaparral habitat on the Mendocino National Forest. Foraging information is verified through Verner and Boss (1980), Perterson (1969) and Udvardy (1977).

Table 5

Common Name	Classification	Methods
Nashville Warbler	insectivore	foliage gleaner; hawking
Yellow Warbler	insectivore	foliage gleaner
Black-throated Gray Warbler	insectivore	foliage gleaner; hawking
MacGillivray's Warbler	insectivore	foliage gleaner; ground probing
Orange-crowned Warbler	insectivore	foliage gleaner; twigs; bark
Wilson's Warbler	insectivore	foliage gleaner; hawking
Black-headed Grosbeak	omnivore	foliage gleaner; picks fruit, buds; ground probing
Lazuli Bunting	insectivore	foliage gleaner; hawking; ground probing
Chipping Sparrow	insectivore granivore	foliage gleaner ground probing
Dark-eyed Junco	insectivore granivore frugivore	foliage gleaner ground probing hawking
Western Tanager	insectivore frugivore	foliage gleaner; hawking picks fruit
Western Kingbird	insectivore	hawking
Ash-throated Flycatcher	insectivore frugivore granivore	hawking foliage gleaner ground probing
Pacific-Slope Flycatcher	insectivore	foliage gleaner; hawking
Dusky Flycatcher	insectivore	hawking
Western Wood Peewee	insectivore	hawking
Calliope Hummingbird	nectar insectivore	from flowers hawking
Rufous Hummingbird	nectar insectivore	from flowers foliage gleaner; hawking
Allen's Hummingbird	nectar insectivore	from flowers foliage gleaner; hawking
Common Poorwill	insectivore	hawking; ground probing
Cliff Swallow	insectivore	hawking
White-throated Swift	insectivore	hawking

Common Name	Classification	Methods
Blue-gray Gnatcatcher	insectivore	foliage gleaning; hawking
Solitary Vireo	insectivore granivore	foliage gleaning

Table 6 list where species would be expected to forage within the chaparral substrate. Some species are listed in more than one category. The cliff swallow and white-throated swift are omitted from the lists as they both hawk flying insects high above the chaparral canopy. The white-throated swift is not known to spend any time on the ground. Foraging information is verified through Verner and Boss (1980).

Table 6		
Ground Level/Low Dense Shrub Cover	Shrub Height Over 5 Feet	Conifer/Deciduous Tree Canopy
Nashville Warbler	Orange-crowned Warbler	Yellow Warbler
MacGillivray's Warbler	Dusk Flycatcher	Black-throated Gray Warbler
Wilson's Warbler	Western Wood Peewee	Orange-crowned Warbler
Black-headed Grosbeak	Western Flycatcher	Black-headed Grosbeak
Lazuli Bunting	Ash-throated Flycatcher	Western Tanager
Dark-eyed Junco	Blue-gray Gnatcatcher	Western Wood Peewee
Common Poorwill	Yellow Warbler	Dusky Flycatcher
Chipping Sparrow	Black-throated Gray Warbler	Ash-throated Flycatcher
Allen's Hummingbird	Black-headed Grosbeak	Western Kingbird
Rufous Hummingbird	Dark-eyed Junco	Blue-gray Gnatcatcher
Calliope Hummingbird		Solitary Vireo
		Pacific Slope Flycatcher

DISCUSSION

Persistence of migrant populations depends on the bird's ability to find favorable conditions for survival throughout the annual cycle (Moore and Simons 1992). Productivity of breeding in temperate areas must be balanced against costs of migration. Migrants must adjust to unfamiliar habitats which vary in suitability, resolve conflicting demands of predator avoidance and food acquisition, and compete with other migrants and resident birds for limited resources (Francis and Cooke 1986). From 1978 to 1987, 75% of the forest neotropical migrants displayed negative trends, and 20 of 25 species showed a significant trend toward declining populations (Finch 1991b). Short distance migrants and resident species nesting in grasslands and scrublands showed consistent population declines (Droege and Sauer 1990), possibly in relation to patterns of drought and population trends of the parasitic brown-headed cowbird. A persistent decline caused by large scale processes, such as conversion of tropical forests, may be masked by drastic local declines on the breeding grounds (Askins et al. 1990).

While most studies have been conducted in the northeastern United States, it is interesting to note that birds that breed in the west reside primarily in riparian habitat and montane forests, rather than extensive western grasslands and shrubsteppe (Terborgh 1989). Because their habitats are restricted in distribution, total populations of western migrants may be much smaller than those of eastern species, making them particularly vulnerable to disturbances and forest fragmentation (Terborgh 1989). Migrant species exhibiting declining populations in California are; yellow warbler, willow flycatcher, Bell's vireo, yellow-breasted chat, bank swallow, purple martin, sharp-shinned hawk, Cooper's hawk, and

Swainson's hawk (Zeiner et al. 1990). These species are recognized as utilizing riparian habitats. England (1990) determined through his observations that riparian habitat has an important influence on those species choosing to breed and nest in chaparral on the Mendocino National Forest. Riparian associated migrants have become restricted to steep, narrow bands of riparian corridors due to fragmentation from agriculture and other land use purposes (USDA 1993).

Fire has always been an important part of the life cycle in the chaparral environment. Fire normally occurs with sufficient frequency that both plants and animals are well-adapted to its passage; some species may require fire-maintained vegetation or habitat for their continued existence (Van Lear and Waldrop 1989). Studies show that to enhance species diversity and attract species with different habitat requirements, prescribed rotational burning to create various age-classes of chaparral substrate is recommended (England 1986). There are contrasting views regarding the time of year to burn with regard to erosion, nitrogen loss, and seed regeneration, but generally, late spring burning is discouraged due to the inability to create fire intensity sufficient to enable seed germination (Shea et al. 1981). Today, fire suppression activities have restricted the natural frequency of burns within the chaparral system, which may in turn adversely affect those species whose persistence depends on its periodic occurrence (Mayfield 1960, Remson 1986).

Type conversion is another management tool used to convert shrublands to grasslands. Studies have shown that if maintained through frequent treatments, birds with grassland affinities are attracted to those areas (England 1990). Consideration for the size and shape of the created tracts is important as the edge replacement between two dissimilar habitat types lessens the overall size of habitat for forest-interior species.

Because cowbirds are associated with edge and agricultural practices, Robinson et al. (1993) suggests that the best management strategy is to maintain large areas of contiguous habitat. He stresses the importance of management of the surrounding landscapes and utilizing methods that discourage increased food source practices. Practices that increase feeding opportunities for brown-headed cowbirds are; mowing of roadsides and campgrounds, establishing corrals or pack stations, and allowing livestock grazing.

Further studies are needed for other geographical locations within the chaparral system to determine optimum fragmentation size and shape, stopover habitat requirements, and rotational burning for age-class management. Further information is also needed on behavioral characteristics specific to those individual species that utilize chaparral.

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